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Towards a more temporally explicit framework for community ecology

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Abstract

Although ecologists have long understood the fundamentally dynamic nature of communities, ecology has until recently seemed to emphasize other aspects of ecological complexity, such as diversity and spatial structure, ahead of temporal variation. Climate change has made studies into the temporal dimensions of community ecology more immediate and urgent, and has exposed the limits of our general understanding about how species interactions change over time. Here, I suggest four specific ways to continue building towards a more temporally explicit understanding of community ecology: 1) by increasing the representation of temporal change in interaction networks, 2) by developing both specific and general insights into event-driven dynamics, 3) by developing and testing sequential hypotheses to describe proposed explanations that unfold over time, and 4) by characterizing seasonal windows of opportunity. A great deal about the temporal dynamics of communities remains uncertain, but temporally explicit studies have the potential to improve our fundamental understanding of how communities function.

Keywords: temporal ecology, phenology, event-driven dynamics, sequential hypotheses, seasonal windows of opportunity, climate change, time-communities, dynamic interaction networks, flying gallop

Introduction

In 1872, the English-American photographer Eadweard Muybridge was hired by Leland Stanford, a former governor of California, railroad tycoon and horse enthusiast, to do a photographic study of animal locomotion. At the time, the precise way a horse moved while galloping was unknown, and the subject of vigorous debate. Because the legs of a galloping horse move too quickly for accurate observation with the unaided eye, previous hypotheses for the gait and posture of a galloping horse were largely based on conjecture and imagination. In order to observe how a horse gallops, Muybridge needed to develop new photographic methods and tools. Prior to the completion of his photographic studies, artists generally depicted galloping horses in a “flying gallop” posture (Fig. 1A), with their front legs extending in front of them, and their hind legs simultaneously extended behind them. Muybridge’s photographs showed horses with a fundamentally different posture when galloping (Fig. 1B). With the first publications of these images (“A horse’s motion scientifically determined,” 1878; Muybridge, 1887), our understanding of animal movement was profoundly changed. As *Scientific American* (1878) wrote at the time, *“Before these pictures were taken no artist would have dared to draw a horse as horse really is when in motion… yet after a little study the conventional idea gives way to truth, and every posture becomes instinct… Mr. Muybridge’s ingenious and successful efforts to catch and fix the fleeting attitudes of moving animals thus not only make a notable addition to our stock of positive knowledge, but must also effect a radical change in the art of depicting horses in motion.“*

As with galloping horses, our understanding of community ecology has historically been influenced by static depictions of inherently dynamic processes. These static representations of how species interact have become a principal part of our ability to conceptualize complex natural systems, and have succeeded in conveying many important insights about the structure of communities. However, like a painting of a horse in motion, our static depictions of communities both reveal and shape our assumptions about how communities work. While static representations of communities have structured community ecology in many ways, ecologists have always understood that the natural systems underlying these static representations are highly dynamic. In his foundational book *Animal Ecology*, Charles Elton (1927) established several concepts that have become central to ecology, including food web diagrams, the biomass pyramid and the Eltonian niche concept. However, this book also includes a chapter devoted to "time-communities", noting that *"animal communities are organized into a series of smaller animal communities, each of which is in action at a different time."* Elton's book makes it clear that the study of temporal patterns in species interactions was central to community ecology from the beginning, and this more temporally explicit perspective developed concurrently with the first depictions of static food webs. These are not contradictory or inconsistent perspectives; rather, they represent ways to examine different aspects of ecological complexity in a more manageable way; emphasizing the structure and spatial organization of species interactions on the one hand, and emphasizing the dynamics and temporal organization of species interactions on the other. Since the early days of ecology, these two perspectives have developed along parallel but uneven paths; until recently, the study of important structural and

spatial issues in community ecology has seemed to outpace the development of a more temporally explicit perspective.

The reality of ongoing climate change has made the study of temporal change in community ecology more immediate and urgent, and has contributed to a resurgence of interest in developing a better understanding of the temporal dimension of species interactions on more fundamental level (Forrest & Miller-Rushing, 2010; Parmesan & Yohe, 2003; Post, 2019; Visser, Caro, Oers, Schaper, & Helm, 2010; Wolkovich, Cook, McLauchlan, & Davies, 2014b; Yang & Rudolf, 2010). Climate change is causing widespread phenological shifts in the timing of life histories (Hua et al., 2016; Parmesan, 2006), and phenological mis-matches have the potential to disrupt species interactions in a community (Both, Van Asch, Bijlsma, Van Den Burg, & Visser, 2009; Kharouba et al., 2018). Although there is a general pattern of advancing phenologies in diverse taxa around the globe consistent with expectations on a warming planet (Parmesan & Yohe, 2003), the variability of phenological responses to climate change is large, complex and often counterintuitive (Chmura et al., 2019; Cleland, Chiariello, Loarie, Mooney, & Field, 2006; Edwards & Yang, 2018; Forrest, 2016; Høye, Post, Schmidt, Trøjelsgaard, & Forchhammer, 2013; Lane, Kruuk, Charmantier, Murie, & Dobson, 2012; Sherry et al., 2007). While the study of phenology has traditionally focused on the timing of life history events for single species, these changes in the timing of species interactions are forcing us to grapple with the complexity of temporal dynamics in community ecology more broadly; the reality of global climate change requires us to consider phenology in a community context. Understanding phenology and the timing of species interactions has never been more important, and the limits of our current understanding are increasingly evident.

In response to this emerging reality, the study of phenology has advanced rapidly in four specific ways. First, the study of phenology has progressed from the historical study of single, annual life history events (such as the day of peak flowering, or the first arrival of migratory birds) to examining phenological changes over multiple stages in a seasonal trajectory or ontogeny (e.g., Inouye, Ehrlén, & Underwood, 2019; Yang & Rudolf, 2010). Second, the study of phenology is moving from pattern to process; increasingly, studies are able to build upon previously documented patterns of phenological change to ask questions about the causes or consequences of those changes (e.g., Chmura et al., 2019; Forrest & Miller-Rushing, 2010; Inouye et al., 2019; Pau et al., 2011; Visser et al., 2010). Third, ecologists are increasingly investigating a wider range of phenological responses, including phenological changes in the fall (e.g., Gallinat, Primack, & Wagner, 2015), phenological delays (e.g., Lane et al., 2012), phenological responses to extreme events (e.g., Jentsch, Kreyling, Boettcher-Treschkow, & Beierkuhnlein, 2009), changes in generation time (e.g., Forrest, Cross, & CaraDonna, 2019), phenological variation in space (e.g., Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016), and individual variation in phenological responses (e.g., Inouye et al., 2019). Finally, the study of phenology is continuing to work towards putting single-species phenology into a multi-species community context (e.g., Both et al., 2009; Nakazawa & Doi, 2012; Yang & Rudolf, 2010).

Along the way, these trends in the study of phenology are also building a more temporally explicit perspective in community ecology. Fundamentally, a more temporally explicit approach to ecology often requires examining smaller slices of time; this is a recapitulation of Elton's "time-communities" concept in a modern guise, and an ecological echo of Muybridge's photographic method. While

examining smaller slices of time is a quantitative change in the way we already do community ecology, approaches that increase the temporal resolution of available data could qualitatively improve our understanding of how communities work. In many systems, these temporally explicit approaches will likely require the application of new methods and technology, and there will certainly be many questions in community ecology for which a temporally explicit approach will remain unnecessary or impossible. Even as he was describing the richness of temporal variation in communities, Elton wrote that temporal variation *"enormously increase(s) the difficulty of studying (them)"*, and even comparatively regular changes in communities *"make the study of this side of ecology excessively complicated."* However, at its best, this approach allows us to see how nature works more clearly than we could otherwise.

Towards a more temporally explicit community ecology

Here I suggest four ways to build towards a more temporally explicit understanding of species interactions in community ecology: 1) by increasing the representation of temporal change in interaction networks, 2) by developing both specific and general insights into event-driven dynamics, 3) by developing and testing sequential hypotheses to describe proposed explanations that unfold over time, and 4) by characterizing seasonal windows of opportunity. These include both conceptual frameworks and methodological tools that emphasize how species interactions change over time.

Temporally explicit interaction networks show changes in community structure

In recent decades, the analysis of community structure in food webs has emphasized taxonomically well-resolved summary datasets, generally compiled over years of careful study in a given location (Dunne, 2006). These datasets have undeniably shaped our current understanding of ecological communities (e.g., Gibert & DeLong, 2017; Williams & Martinez, 2000), and address many of the data quality problems that arose from the analysis of less well-resolved datasets previously (e.g., Hall & Raffaelli, 1997; Martinez, 1991; Paine, 1988; Polis, 1991). However, the degree to which such static summary networks accurately represent species interactions in nature remains unclear (Jordan & Osvath, 2009; Tavares-Cromar & Williams, 1996). Because these networks are generally static, they are unable to represent changes in community structure over time (Fig. 2; Akin & Winemiller, 2006; Berlow et al., 2004; Tavares-Cromar & Williams, 1996; Warren, 1989). Moreover, because they are cumulative, they may reflect summary community structures that have never existed at any point in time (Fig. 2; Closs & Lake, 1994; Jordan & Osvath, 2009; Schoenly & Cohen, 1991). These concerns are not new (e.g., McMeans, McCann, Humphries, Rooney, & Fisk, 2015; Schoenly & Cohen, 1991), and past studies have addressed them by examining time-specific trophic networks in a range of systems (Akin & Winemiller, 2006; Baird & Ulanowicz, 1989; Ceneviva-Bastos, Casatti, & Uieda, 2012; Closs & Lake, 1994; Hart, Stone, & Berman, 2000; Kitching, 1987; Layer, Hildrew, Monteith, & Woodward, 2010; Schoenly & Cohen, 1991; Tavares-Cromar & Williams, 1996; Thompson & Townsend, 1999; Warren, 1989). Many of these studies documented substantial temporal variation in specific food webs, with sometimes profound changes in community composition and structure over time (Baird & Ulanowicz, 1989; Closs & Lake, 1994; Hart et al., 2000; Kitching, 1987; Schoenly & Cohen, 1991; Tavares-

Cromar & Williams, 1996; Thompson & Townsend, 1999; Warren, 1989; but see also Akin & Winemiller, 2006; Ceneviva-Bastos et al., 2012). When compared directly, the structural properties of temporally aggregated networks are often substantially different from any of their time-specific constituents (Jordan & Osvath, 2009; Schoenly & Cohen, 1991; Tavares-Cromar & Williams, 1996; Thompson & Townsend, 1999; Warren, 1989). This suggests that our understanding of food web structure is likely to be strongly dependent on the scale of temporal aggregation in the underlying data in ways that parallel the unintended effects of species or trophic species aggregation (Hall & Raffaelli, 1997; Martinez, 1991). If summary descriptions create artifacts that substantially alter our understanding of food webs, these quantitative differences between time-specific networks and cumulative summary networks would be expected to increase as more data are gathered; in the absence of a more explicit temporal dimension, the continued accumulation of data could have the unintended effect of further obscuring how communities are structured in time.

Despite the broad understanding that many real-world interaction networks change substantially over time, and evidence that the structure of summary networks often differs significantly from that of time-specific networks, relatively few temporally explicit network datasets exist. This may reflect the fundamental challenge of gathering temporally explicit and taxonomically well-resolved species interaction data. While reconciling the widely recognized importance and ubiquity of ontogenetic diet switching in nature and the observation that relatively few studies that have attempted to incorporate them into food web studies, Tavares-Cromar and Williams (1996) noted, *“…likely, the task of including different life stages has proved intimidating.”* Characterizing summary species interactions networks is

already notoriously difficult (Polis, 1991; Polis & Strong, 1996), and many past efforts to develop time-specific food webs illustrate the uncommon combination of sustained data gathering effort and the extraordinary breadth of taxonomic familiarity that has traditionally been required to characterize interactions networks over time. On top of this, it may be more difficult to generalize the insights afforded by time-specific networks. By their nature, time-specific assessments of community interactions are difficult to replicate, instead relying on the inherent value of their larger temporal resolution and scope (Oksanen, 2001). However, past studies show that temporally explicit network analyses are both possible and can offer unique insights, despite the magnified challenge of characterizing species interactions at multiple intervals of time. For their effort, these studies are often characterized by an uncommonly detailed understanding of the dynamics and drivers behind specific food webs, including informed insights about how environmental cycles and the biology of key species affect community dynamics (e.g., Baird & Ulanowicz, 1989; Closs & Lake, 1994; Warren, 1989). Similar insights have emerged from non-trophic interaction networks, including plant-pollinator networks (e.g., Burkle, Marlin, & Knight, 2013; CaraDonna et al., 2017; Olesen, Bascompte, Elberling, & Jordano, 2008), that been described with a more temporally explicit perspective. Studies such as these inform our understanding of how species interactions change over time.

A broader temporally explicit approach to interaction networks could yield new general insights in community ecology. Attempts at generalization are limited in part by the relatively small number of time-specific interaction networks currently available, and the inherent difficulties of meaningfully comparing the dynamics of species with different relevant timescales (Post, 2019; Rahel, 1990; Takimoto,

Iwata, & Murakami, 2009) and studies that use different sampling and analytical methods (Closs & Lake, 1994; Jordan & Osvath, 2009; Schoenly & Cohen, 1991). These are some of the same challenges that caused Lawton (1999) to conclude that *"…community ecology is a mess, with so much contingency that useful generalisations are hard to find."* New methods could help. For example, continuing advances in the application of stable isotope analysis, molecular genetics and remote sensing to community ecology may allow us to characterize time-specific species interactions more rapidly and accurately in the future (Boecklen, Yarnes, Cook, & James, 2011; Carreon-Martinez & Heath, 2010; Corse et al., 2010; Hardy, Krull, Hartley, & Oliver, 2010; McMeans et al., 2015; Nielsen, Clare, Hayden, Brett, & Kratina, 2018; Pompanon et al., 2012; Steenweg et al., 2017; Zellweger, De Frenne, Lenoir, Rocchini, & Coomes, 2019). It seems possible that these new approaches could increase the quality and availability of datasets in ways that substantially improve our ability to generalize how communities change over time. For example, the dynamic nature of species interactions may have implications for the stability and persistence of communities. A growing number of models suggest that consumer responses to spatially structured food webs can contribute to community stability (McCann, Rasmussen, & Umbanhowar, 2005; Wolkovich et al., 2014a), and that temporal structure may play a similar stabilizing role (Kondoh, 2003; McMeans et al., 2015; Takimoto, 2003). The data required to create more temporally resolved interaction networks could also potentially allow for more detailed analyses of stage-structured phenological interaction paths (Yang & Rudolf, 2010) or the geometric analysis of entire community trajectories in time (De Cáceres et al., 2019). Moreover, by representing the dynamic nature of communities more explicitly, time-specific representations help us to consider the effects of

phenological shifts and mismatches in a broader context, where both their direct and indirect effects are more readily considered (e.g., Boggs & Inouye, 2012; Both et al., 2009; Ogilvie et al., 2017). Thus, grappling with the dynamic nature of species interaction networks may help to resolve persistent questions in ecology.

However, it may also be that the value of a temporally explicit approach to interaction networks is less about the statistical analysis of common network properties than it is about the ways we represent and conceptualize how communities work. The ubiquity of static cumulative representations of communities has shaped the way we think about species interactions, and more dynamic representations of these networks have the potential to recast our understanding of how communities change over time. Although an implicit understanding of the dynamic nature of communities has been part of ecology from the beginning of the field, explicitly depicting the dynamic nature of communities is important. Ecologists view the natural world through a conceptual lens of accumulated scientific knowledge and theory that we have built for ourselves. In many ways, this lens allows us to see and understand the natural world with increasing clarity as our field progresses. However, this lens can also distort the complexity of nature as we make the simplifying assumptions that are sometimes necessary to develop meaningful generality. As the conceptual lens of ecology is refocusing on the dynamic nature of communities, continued efforts to document and represent how species interactions change over time lay a foundation for developing a more temporally explicit view of community ecology.

Event-driven dynamics examine our climatic future

Climate change includes trends in mean climatic conditions as well as changes in the timing or magnitude of extreme climatic events (Easterling et al., 2000; Jentsch, Kreyling, & Beierkuhnlein, 2007; Ummenhofer & Meehl, 2017; Wolkovich et al., 2014b). These two aspects of climate change are closely connected; some changes in climatic means are likely to be affected by changes in the frequency or intensity of extreme events, and some changes in the magnitude of extreme events are likely to be driven by the non-stationarity of climatic conditions over time (Bailey & van de Pol, 2016; Easterling et al., 2000; Jentsch et al., 2007; Wolkovich et al., 2014b). For example, increases in the frequency or intensity of heatwaves can contribute to trends in mean annual temperature, while global warming trends may increase the intensity of tropical storm disturbance events (Elsner, Kossin, & Jagger, 2008; Kossin, 2018). These challenges of characterizing the extreme values of climatic distributions and the diversity of ways by which climate interacts with biological systems makes it difficult to objectively define extreme climatic events (Bailey & van de Pol, 2016; Wolkovich et al., 2014b). However, it is clear that extreme climatic events are becoming a larger part of our climatic future (Beniston et al., 2007; Easterling et al., 2000; Goswami, Venugopal, Sengupta, Madhusoodanan, & Xavier, 2006; Groisman et al., 2005; IPCC, 2014), and that those events can have strong effects on ecological communities (e.g., Jentsch et al., 2009; Parmesan, Root, & Willig, 2000; Sergio, Blas, & Hiraldo, 2018).

The study of event-driven dynamics has accelerated as ecologists increasingly recognize the potentially important impacts of extreme climatic events on ecosystems. In 2007, Jentsch et al. advocated for new generation of climate-change experiments focused specifically on the study of climatic events, not trends. Since then, the number of studies focused on climatic events has continued to increase,

with recent studies focused on heat waves (e.g., McKechnie & Wolf, 2010; Siegle, Taylor, & O'Connor, 2018), cold snaps (e.g, Bojorquez, Alvarez-Yepiz, Burquez, & Martinez-Yrizar, 2019; Leriorato & Nakamura, 2019), drought (e.g, Jentsch et al., 2009; Sankaran, 2019), flooding (e.g., Rivas, Spinola, Arrieta, & Faife-Cabrera, 2018; Ujvari, Brown, Shine, & Madsen, 2016; Woodward, Bonada, Feeley, & Giller, 2015), and wildfire events (e.g., Cooper et al., 2015; Hale et al., 2016), among many others. However, while this emphasis has emerged recently in the context of climate change, these questions have deep roots in the study of event-driven dynamics more generally. Many ecosystems were strongly influenced by extreme climatic events, such as El Niño precipitation events, prior to strong human-induced rapid environmental changes (Gibbs & Grant, 1987; Grant & Grant, 1987; Grant, Grant, Keller, & Petren, 2000; Holmgren, Scheffer, Ezcurra, Gutierrez, & Mohren, 2001; Holmgren et al., 2006; Polis, Hurd, Jackson, & Piñero, 1997). Moreover, the contrast between climatic events and climatic trends has parallels with the historical distinction between pulsed versus pressed perturbation experiments in ecology (Bender, Case, & Gilpin, 1984), as well as the study of transient dynamics following a broader range of experimental or natural perturbations (e.g., Hastings, 2004; Jensen, 1982; Jones, Ostfeld, Richard, Schauber, & Wolff, 1998; Piovia-Scott, Yang, Wright, Spiller, & Schoener, 2019; Yang et al., 2010). More than three decades ago, Roughgarden (1989) asked, *"How are ecosystem structure and function influenced by the rare but important events that may occur every century or so?"* This is a general ecological question with a long history, and though it has re-emerged and become more urgent in the context of climate change, previous studies may offer some relevant insights.

317 The detailed study of event-driven dynamics emerges readily from a broader
318 temporally explicit perspective in community ecology. However, because extreme
319 events are often unreplicated and unanticipated by their nature, identifying and
320 evaluating general hypotheses is a central challenge (Bailey & van de Pol, 2016). As
321 a result, the study of extreme events has initially and perhaps necessarily included
322 the accumulation of opportunistic, unique and descriptive studies. Although many of
323 these studies are focused on short-term community responses to singular
324 perturbations (Bailey & van de Pol, 2016), they nonetheless contribute to our
325 broader understanding of event-driven dynamics in nature. The variability of these
326 events, and of community responses to them, create rich opportunities to identify
327 general patterns through synthesis, meta-analysis and coordinated research
328 networks if we are able to characterize the fundamental, shared dynamic features
329 of seemingly disparate events in ways that allow for meaningful comparisons (e.g.,
330 Easterling et al., 2000; Holmgren et al., 2001; Yang et al., 2010). Short time-scale
331 descriptive studies of extreme events have also been followed by longer-timescale
332 studies (e.g., Grant & B.R. Grant, 1996; Meserve, Kelt, Milstead, & Gutierrez, 2003;
333 Stuble, Zefferman, Wolf, Vaughn, & Young, 2017b), manipulative experiments (e.g.,
334 Jentsch et al., 2009; Piovia-Scott et al., 2019; Yang & Karban, 2019), and theoretical
335 models (e.g., Collins et al., 2014; Davis, Grime, & Thompson, 2000; Holt, 2008). For
336 a wide range of episodic perturbations, explicitly examining how communities
337 respond over longer timescales allows us to track their direct and indirect effects
338 across a species interaction network (e.g., Jones et al., 1998; Piovia-Scott, Yang, &
339 Wright, 2017; Yang et al., 2010), and to consider the timing of perturbation events
340 in relation to seasonality and species life histories (Jentsch et al., 2007).
341 Experimental manipulations of extreme events create opportunities to simulate and

anticipate uncommon events, control the frequency and magnitude of events, and infer the causes of community responses. However, such experimental manipulations can be difficult to apply at relevant scales, and experimentally pressed warming manipulations have been shown to underestimate the magnitude of phenological responses relative to observational studies (Wolkovich et al., 2012). Although a greater emphasis on the temporal dimension often seems to come at some expense (e.g., of spatial or taxonomic resolution, or of conceptual generality), the study of extreme climatic events provides a uniquely productive and relevant context in which to explicitly examine the temporal dynamics of community responses to perturbation. These studies, using a range of approaches, have the potential to meaningfully advance our understanding of climate change specifically, and inform our understanding of ecological stability and resilience more generally.

By their nature, events occur during a particular slice of time. Two temporally explicit questions arise as a result: 1) To what extent does the specific timing of an event matter? and 2) Under what conditions do events have persistent effects on communities? Questions about the specific timing of events are relevant to both transient and persistent effects, while questions about the persistence of effects provide a converse perspective on questions about ecological resilience. The degree to which differences in the seasonal or successional timing of events effects their community responses remains unclear. Underlying temporal patterns in organismal life history patterns, species interactions, or abiotic variability all provide the context for strong perturbation events, with consequences in both natural and experimental contexts (Jentsch et al., 2007). For example, the effects of both hurricanes and seaweed subsidies on lizard populations depend on their seasonal timing (Schoener, Spiller, & Losos, 2004; Wright et al., 2013). On a shorter

timescale, the effects of hurricanes on coastal and island communities tends to be larger when the storm surge event coincides with high tide (Schoener, Spiller, & Losos, 2001; Thomas et al., 2019). In general, extreme events during seasonal windows of opportunity (e.g., Yang & Cenzer, 2020) may be more likely to have strong effects on growth or reproduction, as windows of opportunity may also represent important weak-link stages that are potentially vulnerable to perturbation. On an inter-annual scale, many ecological experiments show strong year-to-year variability in results (Stuble, Fick, & Young, 2017a; Stuble et al., 2017b; Vaughn & Young, 2010); this environmental variability can both be caused by event-driven dynamics (e.g., Stuble et al., 2017b), and affect the outcomes of event-driven dynamics (Jentsch et al., 2007). By comparison, the potential for persistent effects resulting from episodic events has been more clearly documented. Numerous examples suggest that ecologically persistent effects could potentially arise from both long timescale transient dynamics (Hastings, 2004) and changes in equilibrium states (Beisner, Haydon, & Cuddington, 2003; Scheffer, Carpenter, Foley, Folke, & Walker, 2001; Scheffer & Carpenter, 2003). While it can be difficult to distinguish between these two mechanisms (Schroder, Persson, & De Roos, 2005), the persistence of effects on ecologically meaningful timescales can often be observed directly. These include persistent changes in habitat (e.g., Brokaw & Grear, 1991; del Arroyo & Silver, 2018; Lloren, Fahrig, Bennett, Contreras, & McCune, 2019); organismal traits (e.g., Hunter & Forkner, 1999; Little, Fisher, Schoener, & Pruitt, 2019; Siegle et al., 2018; Spiller & Agrawal, 2003); the abundance or distribution of organisms (e.g., Spiller & Schoener, 2007; Wernberg et al., 2013); community composition via invasion or extinction (e.g., Davis et al., 2000; McKechnie & Wolf, 2010; Nowicki et al., 2019); and the frequency or intensity

of the perturbation regime itself (e.g., Crain, Tremblay, & Ferguson, 2019; Parmesan et al., 2000). These are certainly not exclusive mechanisms, and many event-driven dynamics reflect the combined effects of multiple dynamic processes. When multiple dynamic processes take place on different timescales (e.g., Takimoto et al., 2009), the study of event-driven dynamics may benefit from the development of temporally explicit sequential hypotheses.

Sequential hypotheses allow for different processes on different timescales

Sequential hypotheses are proposed explanations that include multiple processes that unfold over time. For example, sequential hypotheses allow for explanations that explicitly describe how indirect effects are expected to ramify across networks, or that describe how a community's response to perturbation can include multiple processes that operate on different timescales. A sequential hypothesis avoids necessarily treating processes on different timescales as strictly alternative hypotheses, but instead recognizes that these multiple processes could all be part of a single response dynamic. In the absence of sequential hypotheses, how we interpret the results of an experiment could depend on its timing. For example, if the relative importance of top-down and bottom-up processes changes over time, a short-term experiment could yield different results and implicate different key processes than an experiment conducted over a longer timescale. Thus, evaluating a sequential hypothesis requires evaluating the component parts of each phase, as well as any predictions that emerge from the coordination between them.

Sequential hypotheses have been implicit, or have emerged explicitly over time, in many study systems (e.g., Ostfeld & Keesing, 2000; Yang, Bastow, Spence, & Wright, 2008; Yang et al., 2010). Two specific examples illustrate some of the ways

sequential hypotheses can arise from the indirect effects of strong perturbations and the overlay of multiple processes on multiple timescales. Community responses to periodical cicadas (*Magicicada* spp.) in North American forests provide one example (Fig. 3A). These insects spend 13- or 17-years feeding on the roots of host plants before synchronously emerging as adults at high densities across large geographic areas (Williams & Simon, 1995; Yang & Karban, 2009, 2019). The vast majority of these cicadas will avoid predation, and fall to the ground as a pulse of dead carcasses after reproducing (Whiles, Callaham, Meyer, Brock, & Charlton, 2001; Williams, Smith, & Stephen, 1993; Yang, 2004). This accumulated cicada biomass fertilizes plant growth and reproduction (Yang, 2004, 2008; Yang & Karban, 2019), but also increases damage by mammalian and insect herbivores which preferentially feed on rapidly growing, fertilized plant tissues (Yang, 2008; Yang & Karban, 2019). Thus, the effects of periodical cicadas on their host plants are initially dominated by a long-term, negative direct interaction (*chronic belowground herbivory by cicadas*), followed by a positive, bottom-up, indirect interaction mediated by detritivores and decomposers belowground (*fertilization by the detrital resource pulse*), and a subsequent, negative, top-down indirect interaction mediated by other consumers in the community (*increased consumption by aboveground herbivores*). While community ecologists commonly ask questions about the relative importance of top-down and bottom-up processes (Hunter & Price, 1992; Power, 1992), this example illustrates how the relative importance of top-down and bottom-up processes can change over time. Whereas a simple alternative hypothesis-testing framework could ask *"What are the relative strengths of bottom-up and top-down effects on plants from periodical cicadas?"*, a sequential hypothesis-testing framework considers *"How do the relative strengths of these*

bottom-up and top-down effects change over time?". Such temporal variability in multi-trophic indirect effects may be common (Piovia-Scott et al., 2017). Developing explicitly sequential hypotheses allows us to frame our explanations about how this temporal variation is structured in time, and to propose and test general expectations about changes in the nature of species interactions.

The effects of pulsed resource subsidies on small island communities provides another example illustrating how sequential hypotheses allow us to consider multiple processes operating on different timescales (Fig. 3B, Kenny et al., 2017; Piovia-Scott et al., 2013; Piovia-Scott et al., 2019; Spiller et al., 2010; Wright et al., 2013). In this system, rafts of seaweed occasionally wash up on small rocky islands. This seaweed biomass represents marine primary productivity transported by ocean currents and winds; when deposited on islands, this seaweed becomes a pulsed subsidy to the terrestrial community (Piovia-Scott et al., 2019; Spiller et al., 2010; Wright et al., 2013). This pulsed subsidy affects the interactions between terrestrial plants and their herbivores via multiple processes operating on different timescales (Fig. 3B). In experimental studies, lizards (*Anolis sagrei*) show behavioral responses immediately following the additional of pulsed seaweed subsidies, including rapid changes in foraging behavior and habitat use (Kenny et al., 2017). These changes in lizard behavior correspond with rapid shifts in their diet towards marine-derived arthropod prey (Spiller et al., 2010). This lizard diet shift creates a window of opportunity for terrestrial herbivores, which may benefit from reduced predation as lizards focus on a pulse of marine-derived prey (Piovia-Scott et al., 2019). This *"lizard diet shift effect"* represents an indirect mechanism akin to apparent mutualism (Abrams & Matsuda, 1996) by which pulsed seaweed subsidies can reduce terrestrial herbivory in the short-term (Piovia-Scott et al., 2019). However,

these pulsed subsidies can also increase the density of lizards on islands, either by increasing behavioral aggregation, reproduction or survival (Kenny et al., 2017; Wright et al., 2013). As the availability of marine-derived prey declines and lizard diets shift back towards terrestrial prey, these increased lizard densities can more strongly suppress terrestrial herbivores, reducing herbivory (Piovia-Scott et al., 2019). Thus, this *"lizard numerical response"* mechanism is an indirect pathway by which pulsed subsidies of seaweed can increase terrestrial herbivory on intermediate timescales, by a process akin to apparent competition (Holt, 1977). On longer timescales, subsidies of seaweed biomass can also affect the interaction between terrestrial plants and their herbivores via a third pathway, the "*fertilization effect*". According to this hypothesized pathway, decomposing subsidies of seaweed fertilize nutrient-limited terrestrial islands, enriching the belowground component of these systems. In turn, this fertilization increases the growth and quality of terrestrial plants, increasing rates of herbivory. This process is a strong driver of observed herbivory rates in chronically subsidized locations (Piovia-Scott et al., 2013), and may also play a role in responses to more strongly pulsed subsides. Thus, this hypothesized community response includes three processes that occur on different timescales. In this example, a simple alternative hypothesis framework could ask *"What are the relative strengths of these three hypothesized indirect pathways resulting from pulsed seaweed subsidies?"*, while a sequential hypothesis framework considers *"How does the relative importance of these three hypothesized indirect pathways change over time?"*. Developing a sequential hypothesis requires a more detailed and specific explanation for the effects of a perturbation over multiple timescales, including aspects that would be difficult to explain without a temporally explicit, multi-stage hypothesis.

As with any hypothesis, sequential hypotheses should be evaluated relative to alternatives, potentially including both alternative sequential hypotheses as well as alternative simple (i.e., single-stage, nonsequential) hypotheses. Also, as with any hypothesis, sequential hypotheses are likely to evolve over time with the addition of new information or insight. The unique value of a sequential hypothesis is in its temporal specificity; by encouraging researchers to propose explanations that include multiple linked processes that unfold over time, sequential hypotheses extend the temporal scope of studies to explicitly examine and evaluate our expectations of how species interactions change.

Sequential hypotheses are narrative by their nature; they propose an explanation that incorporates a series of connected events. Sequential hypotheses seek to extend conventional hypotheses to allow for a more explicit consideration of time, linking event-driven dynamics and dynamic interaction networks with a stronger hypothesis-driven approach.

Seasonal windows of opportunity put phenological shifts in context

In 1957, G. Evelyn Hutchinson proposed a conceptual model of the ecological niche as an *"n-dimensional hypervolume… every point of which corresponds to a state of the environment which would permit the species* S_1 *to exist indefinitely."* This formalization of the niche concept built upon the niche concepts of Grinnell (1917) and Elton (1927), and established an explicit separation between the abstract concept of a niche in environmental dimensions versus the mapping of that niche onto the physical landscape (i.e., the "biotop", *sensu* Hutchinson 1957). This duality between the conceptual niche and the physical instantiation of the niche, and the ways in which those two realms are linked, continues to have relevance and

implications for ecology today (e.g, Colwell & Rangel, 2009). Considering how this duality changes over time has emerged as one of the ways in which modern ecologists are extending the utility of the Hutchinsonian niche concept. In a list of the key limitations of this niche model, Hutchinson (1957) noted that, *"The model refers to a single instant of time."* However, in much the same way that Hutchinson's niche concept can be mapped onto specific locations in heterogeneous space, the niche concept could also be mapped onto specific slices of time in dynamic environments. In this sense, Hutchinson's duality becomes a *tri*ality as the combination of factors that define the conceptual niche are mapped onto both space and time. This niche concept could be further extended to represent both temporal and spatial changes over ecological and evolutionary timescales. On an ecological timescale, the physical locations where niches map onto the biotop can change over time as a result of temporal variation in the environment. On an evolutionary timescale, the fundamental niche itself can change over time, as a result of organismal (i.e., evolutionary) change (Colwell & Rangel, 2009). These changes are not exclusive, and reflect the dynamic nature of the niche concept.

Seasonal windows of opportunity are potentially relevant to the Hutchinsonian niche concept, but approach this conceptual territory from a different direction. Seasonal windows of opportunity are intervals of time in which an organism has improved prospects for achieving key life history objectives such as growth or reproduction (Fig. 4, Yang & Cenzer, 2020). Although windows of opportunity have been described on daily to inter-decadal timescales, seasonal windows of opportunity emphasize the timing of life history processes within a year. These seasonal windows of opportunity provide moving temporal targets for phenological cueing strategies with potential fitness payoffs (e.g., Farzan & Yang, 2018; Rafferty & Ives,

2011; Valdés & Ehrlén, 2017), similar to “phenological niches” (Post, 2019; Wolkovich & Cleland, 2011, 2014). Identifying seasonal windows of opportunity for specific organisms allows us to examine the potential consequences of phenological shifts and mismatches, putting the fitness consequences associated with the timing of key life history processes into a broader seasonal context (e.g, Fig. 4, see also Yang & Rudolf, 2010). The studies required to identify seasonal windows of opportunity may also suggest hypotheses about the specific combinations of biotic and abiotic conditions that allow for successful development. Subsequent experiments to identify the combination of conditions that limit seasonal windows of opportunity could provide an entryway to better understand the mechanistic bases of these windows.

Seasonal windows of opportunity and the Hutchinsonian niche concept both aim to identify favorable combinations of conditions, and endeavor to map these combinations of conditions in the real world. While the Hutchinsonian niche concept has traditionally emphasized the spatial dimension, seasonal windows of opportunity emphasize the temporal dimension. If we accept that the Hutchinsonian niche concept could be extended to include a more explicit temporal aspect, seasonal windows of opportunity represent a component of the Hutchinsonian niche mapped onto specific slices of time. However, whereas the Hutchinsonian niche concept is defined by the combination of conditions that allow a species to persist indefinitely, seasonal windows of opportunity emphasize the transient nature of favorable conditions in many systems. Where the Hutchinsonian niche concept begins in the abstract realm of *n*-dimensional hyperspace and imagines mapping this concept onto the physical world, seasonal windows of opportunity will more commonly begin in the physical world, and seek some conceptual consequence

afterward. While it seems plausible that an organism's ability to consistently capitalize on transient seasonal windows of opportunity could contribute to the persistence of a species, more concrete links between these two related concepts remain uncertain.

The experimental methods used to identify seasonal windows of opportunity can be simultaneously straightforward and complex (Farzan & Yang, 2018; Yang & Cenzer, 2020; e.g., Yang & Rudolf, 2010). These studies are potentially straightforward in the sense (and to the degree) that studies that assess the performance of an organism at any given point in time can be conceptually simple to design and execute. They are potentially complex in the sense that this experimental motif is then repeated at intervals throughout the season, with each repetition of the core assessment occurring under changed biotic and abiotic conditions. The dynamic pattern describing how an organism's developmental prospects change over annual time represents a seasonal performance landscape, with peaks and valleys representing periods of improved or constrained performance, respectively. Much like Eadweard Muybridge's photographic studies of animal locomotion, a series of repeated ecological observations, each potentially unremarkable on its own, offers the potential for emergent insights when structured in time and examined in series.

Studies that identify seasonal windows of opportunity can suggest at least three kinds of follow-up studies. First, subsequent studies may ask about the *causes* of observed seasonal windows of opportunity. What are the seasonally variable biotic or abiotic factors that constrain and structure developmental potential in time? What are the phenological cueing strategies that proximately determine the timing of organismal life history events? A second kind of study asks about the *dynamics* of

seasonal windows of opportunity. How do seasonal windows of opportunity vary across multiple years or across the range of a species? How is climate change altering the timing of seasonal windows of opportunity across years? Finally, studies could ask about the ecological and evolutionary *consequences* that emerge from seasonal windows of opportunity. For a single species, how do seasonal windows of opportunity for one life history stage interact with those of other stages (e.g., germination and flowering)? In a community context, how do seasonal windows of opportunity for one species interact with those of other species (e.g., predators and prey)? What are the fitness costs associated with phenological shifts and mis-matches?

It is clear that phenology is a process that occurs across development (Chmura et al., 2019; Inouye et al., 2019; Yang & Rudolf, 2010). The study of seasonal windows of opportunity may further motivate the examination of phenology across entire life history trajectories, and could offer a framework to examine both the causes and consequences of phenological shifts in a community context.

Conclusions

The timing of species interactions matters in community ecology because ecological communities are inherently dynamic. As careful observers of nature, ecologists have always understood this at an intuitive level. Despite this (or perhaps because of this), there is a great deal about the temporal dynamics of communities that remains uncertain. As climate change continues, an increasing motivation to better understand the temporal dimension of communities has intersected with advances in the methods and technology to examine small slices of ecological time. At this intersection, there is the potential to improve our fundamental understanding of

how communities function. By analogy, it could be that our understanding of ecological communities today is akin to the way artists in the late 19th century understood the galloping horse. In many cases, they likely understood the general movement of horses quite well, intuitively and via direct experience, and were able to successfully apply this general knowledge in useful ways. However, when attempting to explicitly depict a galloping horse in mid-stride, even experienced artists of the time were forced to rely on conventional wisdom to fill in the details. Our modern understanding of how a horse gallops didn't emerge until a strong motivation to better understand the movement of the galloping horse intersected with the development of new methods and technology to explicitly examine small slices of time. Prior to this, paintings of galloping horses represented the best available understanding of the time, but poorly represented the dynamic aspect of nature. Similarly, ecologists today understand the general dynamic nature of communities quite well, both intuitively and via direct experience, and are often able to successfully apply this general knowledge in useful ways. However, relatively few studies have aimed to understand how species interactions change over time in a detailed and temporally explicit way. As we fill in the details that occupy smaller slices of time, we are progressing towards a more complete and dynamic understanding of how ecological communities actually work.

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Figure 1. (a) Pre-1872 paintings illustrating the “flying gallop” posture (row-wise from the top left): *A Grey Horse Galloping in a Field* by George Stubbs; *Baronet with Samuel Chifney up* by George Stubbs; *A Grey Arab Stallion Galloping with Dogs* by Alfred de Dreux; *Galloping Horse* by Alfred de Dreux; *Foxhunting, Encouraging Hounds* by John Frederick Herring, Sr.; *The Baron with Bumpy Up at Newmarket* by John Frederick Herring, Sr,; *Yoi Yoi! At Him Hannibal* by Henry Thomas Alken, Sr.; *On the Scent Foxhunting* by Samuel Henry Alken; *Wild Dayrell, Winner of the Epsom Derby, 1855* by Samuel Henry Alken; *Thomas Mellish on Saucebox* by Benjamin Marshall; *Le Derby de 1821 à Epsom* by Theodore Gericault; *Mameluke Horse* by Carle Vernet. (b) *The Horse in Motion* by Eadweard Muybridge.

Figure 2. (a) A hypothetical species interaction network. Because taxonomically well-resolved datasets often reflect compiled observations of species interactions accumulated over many years of detailed study, the resulting network structure may not accurately represent the realized structure of species interactions at any single point in time. (b) A diagram of phenology in a community context. One way to add an explicit temporal dimension to interaction networks would be to examine the changing structure of interaction networks during specific slices of time. The data requirements for this kind of analysis are high; here we show hypothetical patterns of development for six species in a community (shown on the vertical axis) over twelve time points (shown on the horizontal axis). Here, we interpret this figure on an annual scale, with time steps corresponding to months in a year, in order to examine seasonal changes in the structure of species interactions. However, this approach could also be applied to other timescales; for example, these time points could represent intervals in a daily cycle if examining diel changes in community

composition or larger timescales (e.g., years or decades) if examining changes in the structure of species interactions over an inter-annual timescale. Each species is represented by a hue; within each species, developmental stages are represented by differences in saturation. The absence of a species at particular time point corresponds to periods of relatively low interactivity in the community; on different timescales, these periods of low interactivity could be caused by dormancy, diapause, seasonal migration or local extinction, for example. (c) A temporally explicit network representation of stage-structured species interactions over time (see also Yang & Rudolf, 2010). The graph in each frame represents the structure of species interactions in the community at a single time point; the set of graphs together represents the temporal dynamics of species interactions in the community. Point size corresponds to the developmental stage of each interacting species. (d) An alternative diagram of phenology in a community context, with phenological shifts from the diagram shown in panel *b*. These phenological shifts are consistent with the range of observed phenological responses to climate change. In this alternative diagram, species 1 and 6 show unchanged phenological trajectories. Species 2 shows an advancement of one time step, while species 3 shows a phenological delay of one time step. Species 4 shows a change from one generation to two generations per year, while species 5 shows an accelerated, temporally compressed developmental phenology. (e) A temporally explicit network representation of stage-structured species interactions over time corresponding to the alternative dataset shown in panel *d*. In this figure, the structure and dynamics of species interactions have changed in multiple ways; in nature, the effects of these changes would be likely to reciprocally influence the evolution and ecology of phenological responses to climate change.

Figure 3. Applying sequential, as opposed to strictly alternative, hypotheses to examine the timing of species interactions in communities in two systems. The diagrams in each panel represent hypothesized interaction networks. From a conventional perspective, these could each represent strictly alternative hypotheses on their own (labeled as H_1, H_2, and H_3). Conversely, from a more temporally explicit perspective, they could represent time-points in an integrated sequential hypothesis (labeled as t_1, t_2, and t_3). (a) The dead bodies of 13- and 17-year periodical cicadas fall to the ground each generation, creating a detrital pulse. As their collective biomass decomposes, a pulse of nutrients becomes available to plants, fertilizing the soil and increasing plant growth (Yang, 2004, 2013; Yang & Karban, 2019). However, these fertilized plants were preferentially consumed by mammalian and invertebrate herbivores (Yang, 2008; Yang & Karban, 2019). Solid arrows indicate the direction of mass or energy flow from resource to consumer, dashed arrows indicate the hypothesized relative strength of top-down and bottom-up effects under each hypothesized scenario. Red arrows indicate the direct bottom-up fertilization effects of the detrital pulse on plants; blue arrows indicate the consumption of plants by herbivores. The first diagram (labeled H_1 or t_1) shows chronic belowground root herbivory by periodical cicadas, while the second diagram (labeled H_2 or t_2) shows detrital fertilization-driven bottom-up effects, and the third diagram (labeled H_3 or t_3) shows stronger top-down effects mediated by other herbivores. (b) Pulsed subsidies of seaweed can have multiple effects on small island communities (Kenny et al., 2017; Piovia-Scott et al., 2013; Piovia-Scott et al., 2019; Spiller et al., 2010; Wright et al., 2013). In particular, pulsed seaweed subsidies could affect plant-herbivore interactions in at least three ways. First, under the *"lizard diet shift"* hypothesis labeled "H_1 or t_1", lizards respond the

seaweed subsidy with a behavioral diet shift towards increasingly marine-derived prey, thus reducing their consumption of terrestrial herbivores, and indirectly increasing measures of herbivory. Second, under the *"lizard numerical response"* hypothesis labeled "H_2 or t_2", local lizard densities increase due to increased survival or reproduction in the presence of a pulsed seaweed subsidy, ultimately increasing the consumption of terrestrial herbivores and decreasing measures of herbivory. Third, in the *"fertilization"* hypothesis labeled "H_3 or t_3", the decomposition of seaweed subsidies fertilizes the soil, increasing plant quality and measures of herbivory. In these diagrams, solid arrows represent the direction of mass or energy flow from resource to consumer, while dashed arrows indicate the hypothesized indirect effect of the seaweed subsidy on herbivores under each scenario. Red arrows indicate resource-consumer interactions related to the indirect bottom-up effects of the detrital pulse on herbivores, while blue arrows indicate resource-consumer interactions associated with the indirect top-down effect of lizards on herbivores.

Figure 4. Seasonal windows of opportunity represent intervals in time when organisms experience improved prospects for advancing their life history objectives, constrained by the combined effects of seasonally variable biotic and abiotic conditions acting independently or in combination (Yang & Cenzer, 2020). In the sense that they are limited by the combined effects of multiple factors, these seasonal windows are a temporally explicit analog of the *n*-dimensional Hutchinsonian niche concept. Here we illustrate the seasonal windows of opportunity associated with a simplified, hypothetical organism whose expected fitness prospects are determined by the combined effects of seasonally variable (a) temperature and (b) precipitation. The seasonal pattern of temperature and

precipitation presented here are based on actual monthly means for Davis, California, USA. Here, the fitness effects of temperature and precipitation are modeled with a Gaussian distribution centered on an arbitrary optimum temperature and precipitation value. Favorable abiotic conditions for this hypothetical species are shown in green; unfavorable conditions are shown in yellow or blue. (c) The resulting seasonal fitness landscape (shown in red) represents the combined fitness effects of temperature and precipitation scaled as the product of the two fitness dimensions. The two periods in the year when favorable climatic conditions overlap define the seasonal windows of opportunity in this example. Although this example shows two seasonally variable abiotic dimensions for simplicity, seasonal windows of opportunity are likely to be structured by *n*-dimensions more generally, including both biotic and abiotic factors.

Figure 1.

(a)

(b)

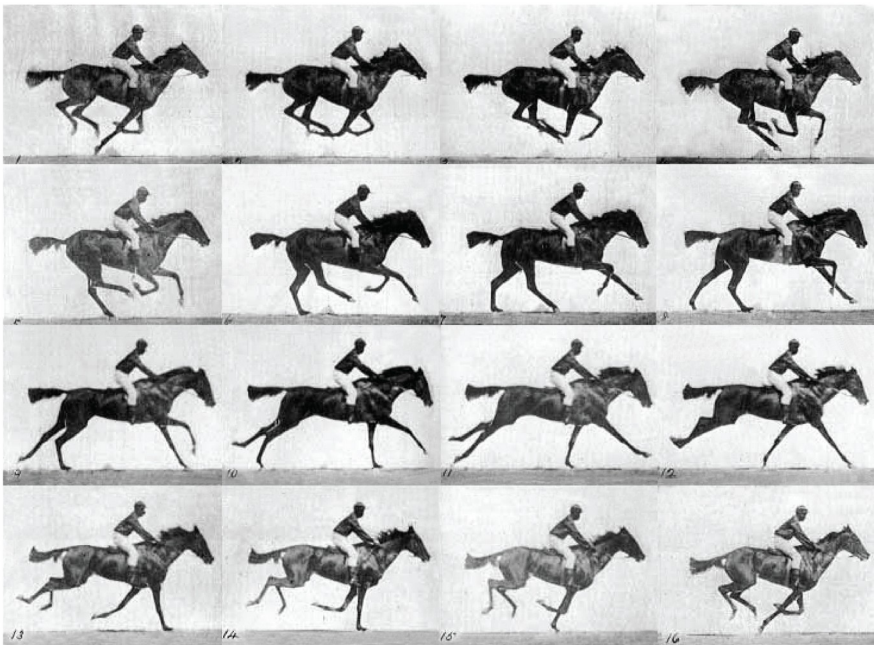


Figure 2.

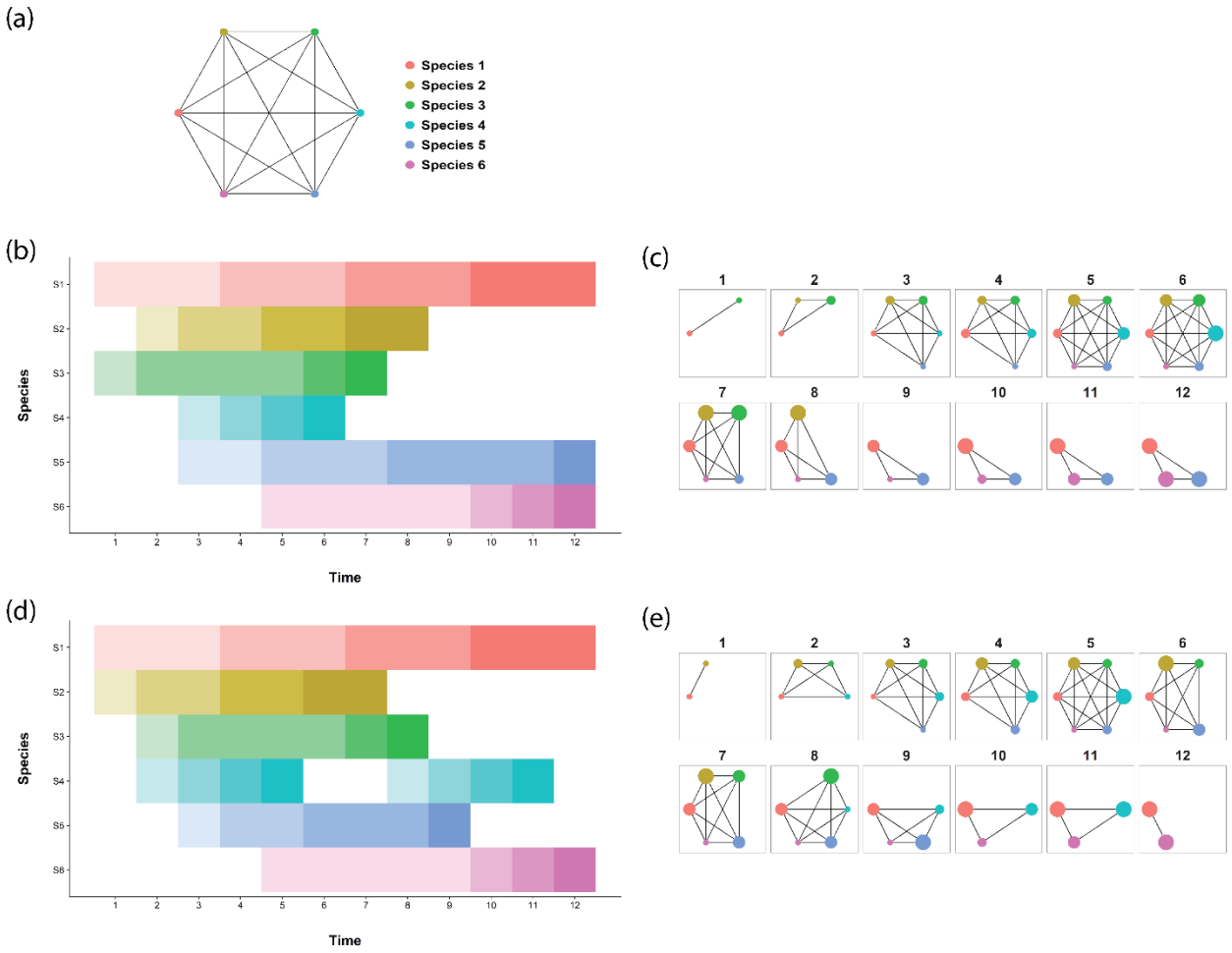
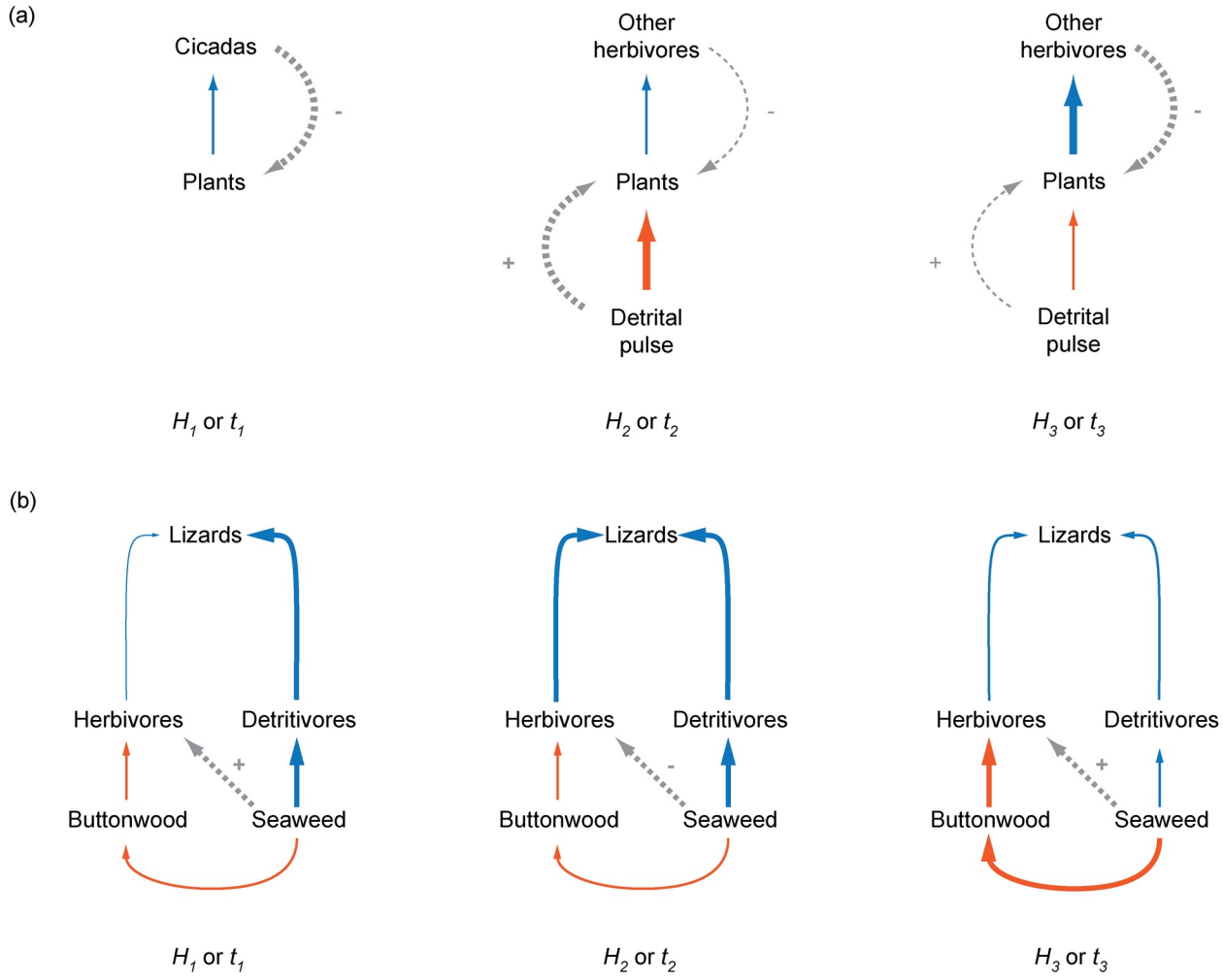

(a)
Species 1
Species 2
Species 3
Species 4
Species 5
Species 6
(b)
Species
Time
(c)
(d)
Species
Time
(e)

Figure 3.


(a)
Cicadas
Plants
-
Other herbivores
Plants
Detrital pulse
+
-
Other herbivores
Plants
Detrital pulse
+
-
H_1 or t_1
H_2 or t_2
H_3 or t_3
(b)
Lizards
Herbivores
Detritivores
Buttonwood
Seaweed
+
Lizards
Herbivores
Detritivores
Buttonwood
Seaweed
-
Lizards
Herbivores
Detritivores
Buttonwood
Seaweed
+
H_1 or t_1
H_2 or t_2
H_3 or t_3

1257 **Figure 4.**

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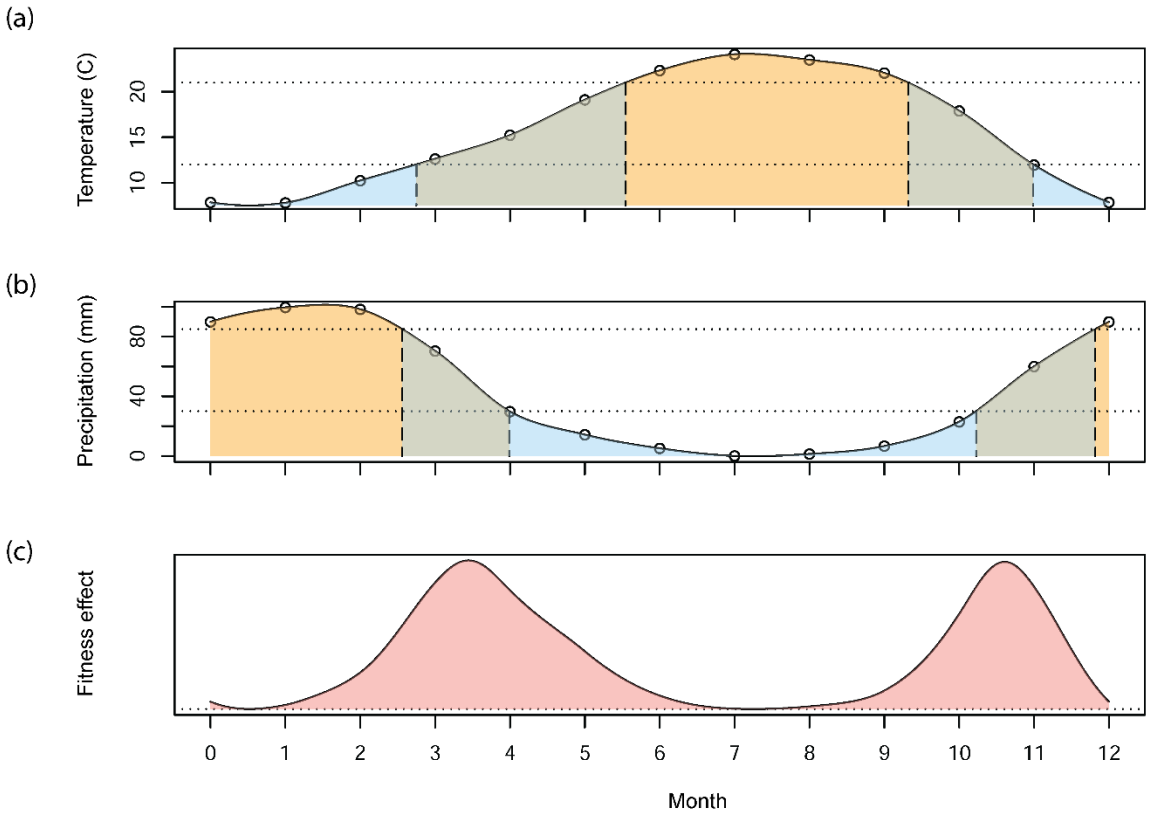

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